THE OVARY AND EMBRYO OF CYRTANTHUS SANGUINEUS

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(WITH PLATE XXIV AND THREE TEXT FIGURES)

Cyrtanthus sanguineus Hook. (Amaryllidaceae) is one of the 37 species credited to the genus. It was first figured in the *Botanical Magazine* (1), and was copied by PAX (2) in his monograph of the family. The genus is restricted to South Africa. *C. sanguineus* and two other species were procured by Dr. C. J. CHAMBERLAIN from the Botanical Garden at Durban, a garden which, like most of those of the colonies, is supported by the nursery trade. The plants are not raised from seed in the garden, but are brought there after being dug up from places in which they grow naturally. The plants secured by Dr. CHAMBERLAIN have been growing in the greenhouses of the University of Chicago. The first blossoms appeared in the winter of 1912-1913. They were hand-pollinated, and from the ovaries and embryos thus derived the present study was made.

Cyrtanthus sanguineus has a tunicated bulb about two inches in diameter. The leaves are thick and leathery, of a bright green color, and about a foot long. The epigynous flower is 3-4 inches in length, and of a rich coral color, almost crimson. The perianth tube is either suberect or decidedly curved, and the upper half of its throat is about one inch in diameter. The stamens are uniseriate and slightly exserted; the filaments are incurved and the anthers are oblong. The ovary is 18 cm. long and 6 cm. in diameter. The ovules are campylotropous. In an ovary of about 12 ovules only 6 or 7 develop to maturity.

Ovary

The material was taken at different ages, killed in chromacetic fluid, and the sections stained in safranin and gentian. All the drawings were made with the help of an Abbé camera lucida.

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The ovary is composed of three carpels. I found two different arrangements of their vascular bundles according to location. In the region of the lateral fusion of the carpels, there are three bundles grouped as one. All are collateral; the outer one is ectophloic, and the other two are so arranged that their xylem masses face each other (text fig. 1). The strands at the midrib of each carpel appear in three distinct groups; the outermost one consisting of a single collateral ectophloic bundle; the innermost one of two bundles with their xylem masses facing; and the intervening group composed of two double bundles, the degree of approximation of which differs at different levels in the carpel. One of the levels is shown in text fig. 2. This peculiarity of arrangement is probably due to the curving of the edge of the carpels to form the closed ovary. A closer study led to an explanation of the different groups of bundles, and showed that each organ of the flower is supplied from these vascular strands. Text fig. 3 is a diagram of the flower, the dotted line representing the outline of the

FIG. 1.—Showing the vascular arrangement at the fusion of the carpels.

ovary. It can be seen that the abortion of the stigmas occurred opposite the region of the fusion of carpels. On tracing their bundles downward into the ovary, they are found to be derived from the primary groups in the carpel. Lower still, these bundles fuse with those of the flower stem.

Noticing the frequent occurrence of stomata on the inner surface of the carpels, I was interested to know the relative number per unit of area in comparison with the outer surface. I found the relation to be as 8:5 in favor of the inner side. This is contrary to what we should expect, for in the foliage leaves of *Cyrtanthus* the stomata are more numerous on the abaxial surface.
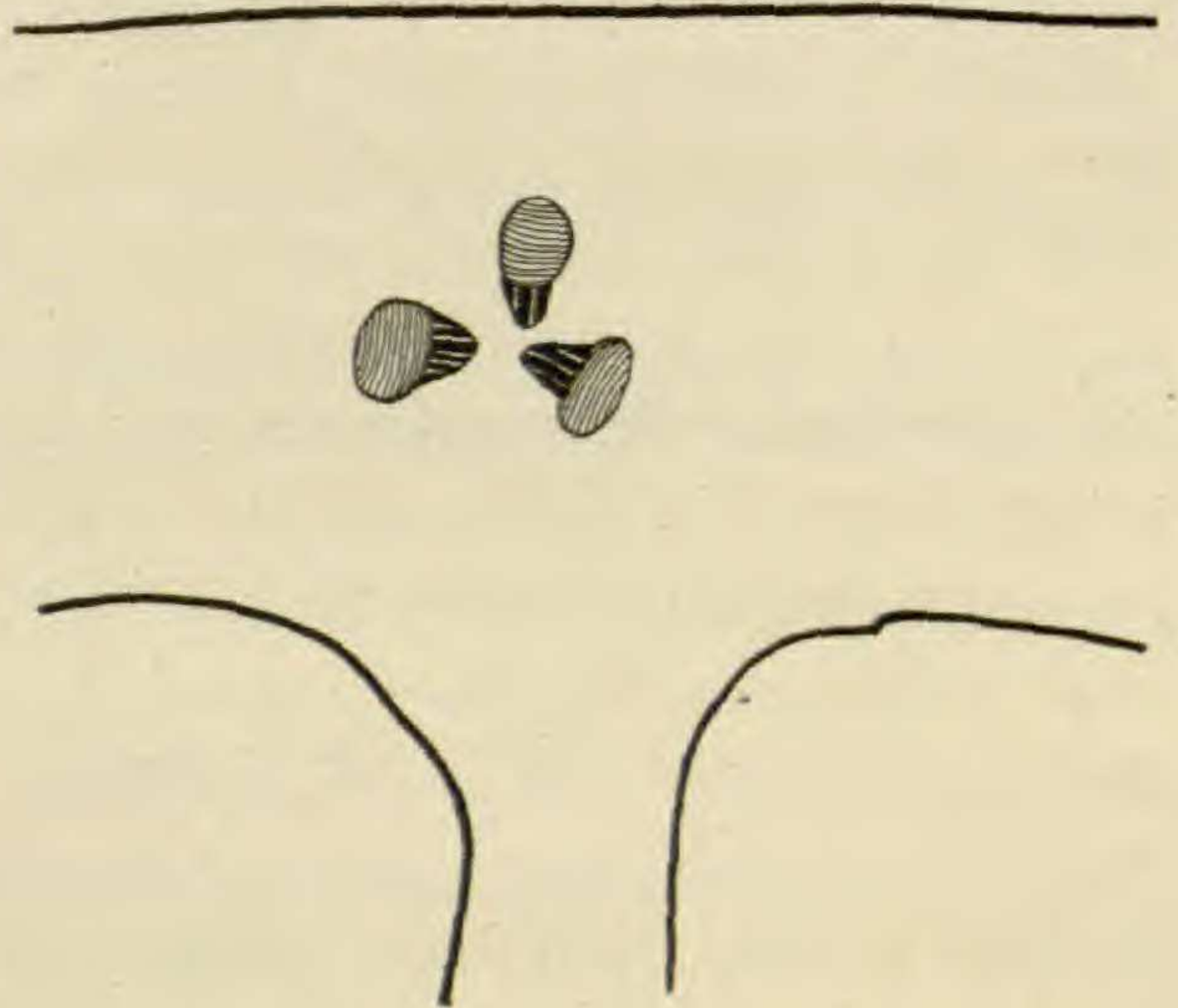
Some of the ovules which were killed in the early stages were examined and found to contain an embryo sac of the lily type. The
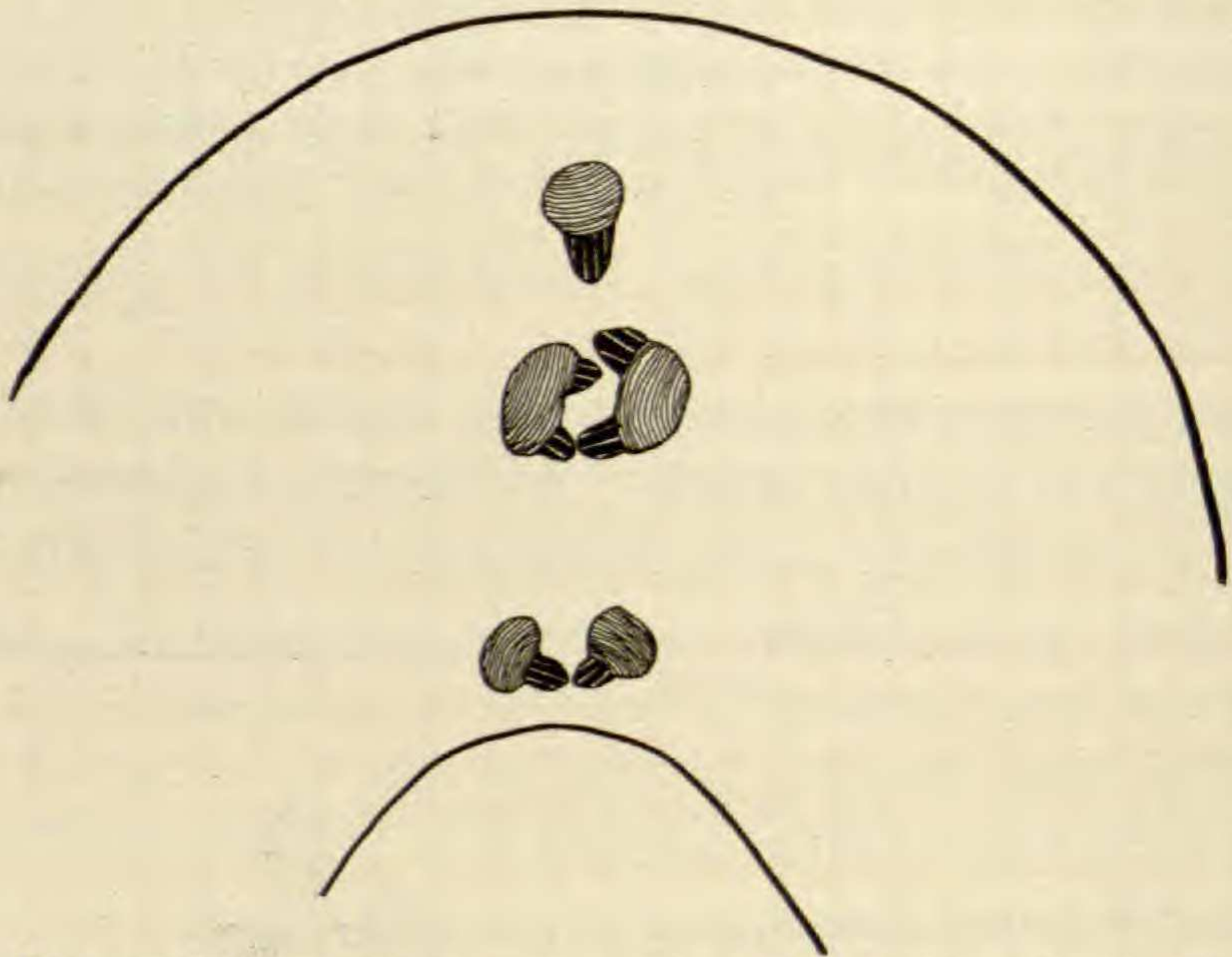

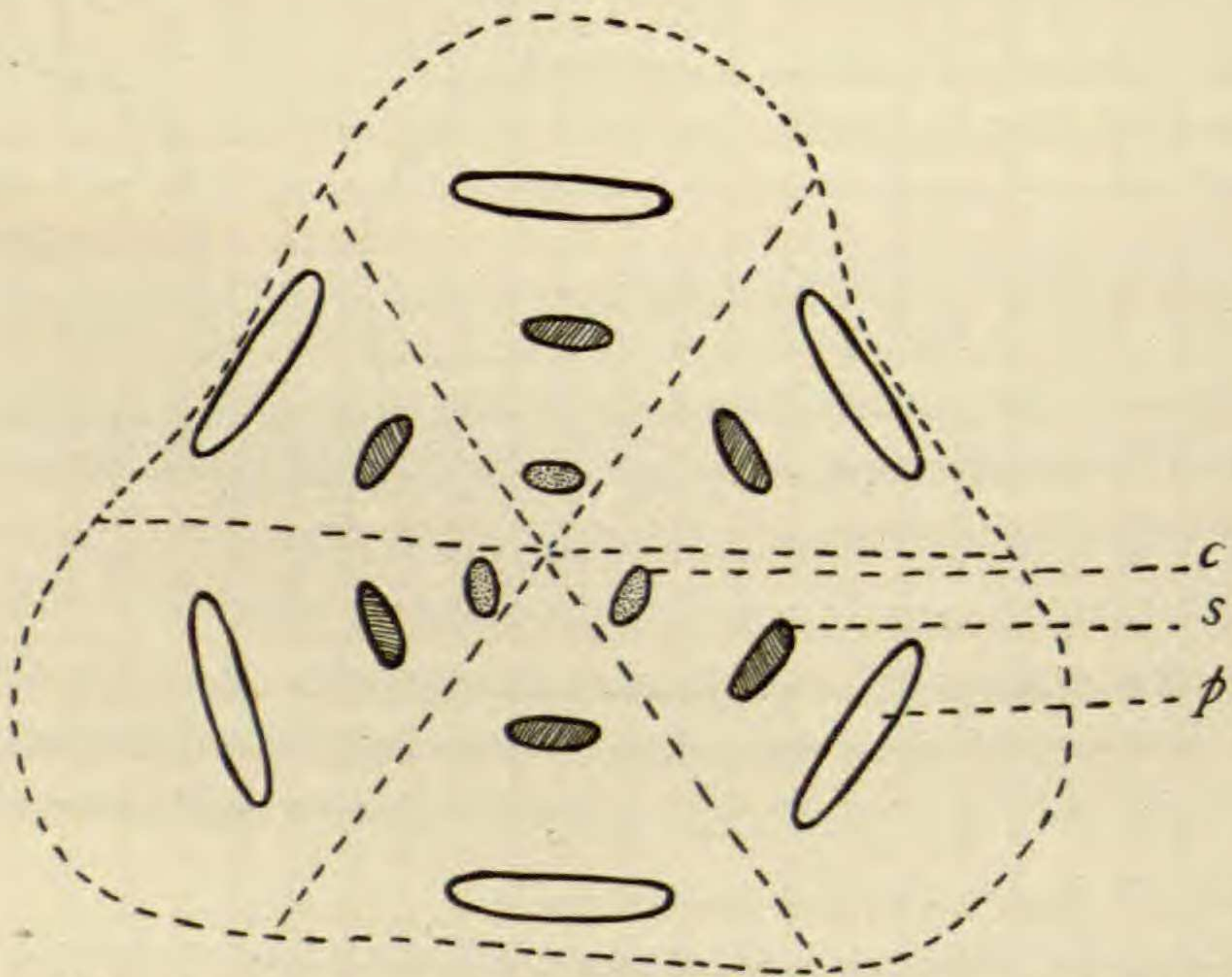FIG. 2.—The vascular arrangement at the midrib of the carpel

FIG. 3.—Diagram of a flower of *Cyrtanthus* against the ovary (dotted line), showing the relation between the vascular conditions and the parts of the flower; *p*, petals; *s*, sepals; *c*, carpels.

antipodals, synergids, and egg showed no departures from this type in the mature stage of the gametophyte; the development up to this stage was not seen.

Embryo

The literature of the embryos of monocotyledons is extensive but not satisfactory. The "sheath" was recognized, of course, early in the history of the study, and was presumed to be a single cotyledon, giving the name to the whole class. Besides the presence of the single cotyledon, early investigators were so impressed with the large amount of endosperm or "albumen," as they called it, occurring outside the embryos in such seeds, that they also called them "albuminous." As to the origin and nature of the cotyledonary sheath, various opinions are expressed, which fact perhaps demonstrates that there are various modes of origin. The earliest writers, HANSTEIN (3) and FAMINTZIN (4), described the embryo of *Alisma Plantago*, in which the cotyledon is terminal in origin. HEGELMAIER (5) describes it in some cases as arising from a cell near the tip, and being pushed into the terminal position by later development. SHAFFNER (6) says that in *Sagittaria* the cotyledon arises from the terminal cell of the proembryo. CAMPBELL (7) finds the same condition in *Naias;* the same author in his study of *Lilaea* (8) says that the sheath is not at first an enveloping organ, but that it becomes such by the lateral growth of its margins; and the same facts are repeated for the Araceae (9). WITTMACK (10) in his monograph on the Bromeliaceae has a drawing of a longitudinal section of the embryo of *Guzmannia tricolor*, taken through the center in such a way as to show the elongated side of the sheath on one side and the shorter side on the other. He calls the long side the "scutellum" and the short side the "cotyledon." There is nothing in his figure to show that scutellum and cotyledon are not one and the same structure, and yet it would seem that so reliable an investigator must have had some reason for applying the two terms in this way. BILLINGS (11) says that the cotyledon is terminal in origin, that the middle segment of the three-celled proembryo gives rise to all the other organs, and that before the stem tip is differentiated, the cells surrounding the area where it is to arise grow up into a ridge of tissue, which in the mature embryo incloses the growing point completely. Here the author seems to imply (1) that the sheath does not completely inclose the growing point in its inception, and (2) that the sheath is not the cotyledon, in the latter respect agreeing with WITTMACK.

A new impulse was given to the study of embryology when COULTER and CHAMBERLAIN began the revision of their *Morphology of gymnosperms* (15). Especially was the impulse felt among the cycads. Cycads were collected from the oriental and occidental tropics, and all phases of their life history investigated. The dicotyledonous nature of the cycadean embryo was demonstrated for all of them, even that of *Ceratozamia* (12, 13), which had been reported as having a single cotyledon. But while these embryos were shown to be normally dicotyledonous, exceptions to dicotyledony were seen to be by no means rare. The case of *Ceratozamia* was proved to be the result of abortion; but in *Microcycas* a condition was found in which the cotyledons were fused to such an extent that the author of the investigation referred to the fused structure as a "sheath," and expressed the suspicion that monocotyledony, even in angiosperms, might have arisen in both these ways: suppression, as in *Ceratozamia*, and fusion, as in *Microcycas*. COULTER and CHAMBERLAIN, in their chapter on evolutionary tendencies (15), seem to give credence to this suspicion by requesting Sister HELEN ANGELA to illustrate her views on the subject of the primitiveness of polycotyledony and the tendency to reduce the number of cotyledons.

From the material at my disposal, I was able to procure embryos in two different stages of development. The younger one was found to consist of an enveloping sheath, still meristematic and with four distinct lobes at its apex. Each lobe has its own vascular strand, four separate strands arising from the four poles of the root. The lobes are approximately equal in size at this stage, but not absolutely so, as can be seen from fig. 2. At the base of the sheath is the region from which the stem tip will arise later; at this stage it is not meristematic. Figs. 1 and 2 of the plate are sketches of the exterior and interior of the embryo at this stage, and fig. 3 is a cross-section which illustrates the irregular growth in thickness of the sheath, the region which bears the vascular strands resisting the pressure from without and giving the appearance of lobes and a four-sided aperture.

The second embryo studied (fig. 4) is older than the one just described. The sheath now consists of two regions, a lower portion

which still envelops the growing point, and a long upper projection which has resulted from the greater growth in length of one side of the sheath. The tip of the shorter, aborted side of the sheath is seen at *a* in figs. 4, 5, and 15. The vacant space in this older embryo, unlike that of the younger, which was four-lobed, is now reduced to the narrow slit represented by *s* in figs. 13 and 14. The vascular conditions are indicated in fig. 5. In the lower region of the sheath (the completely enveloping region below the abortion) each side has two vascular strands, making four in all (figs. 8–13), which arise independently from the cotyledonary node and enter the two differentiated sides of the sheath, just as happens in many dicotyledonous seedlings (figs. 5 and 7). Near the tip of the lower or aborted side of the sheath, the vascular strands from that side abruptly enter the region of the extended side, and fuse with the vascular strands of that organ.

At this stage of development, the growing point has differentiated the first and second leaves, the first arising on the side corresponding to the aborted side of the sheath, and the second one about opposite the first. All are closely pressed upon by the growing sides of the sheath. These arrangements are shown in figs. 5 and 10. The root cylinder is tetrarch (fig. 6).

Discussion

As was remarked before, the amount of endosperm in the seeds of *Cyrtanthus* is very great in proportion to the size of the embryo. This makes it difficult for the embryo to develop its organs to their full extent. I have noted how the originally large space within the sides of the sheath is reduced, little by little, as growth progresses, to a very small space (*s*, figs. 3, 13, and 14). Following out this process in thought, it is not difficult to imagine how the early condition indicated in fig. 3 might easily be changed into that of figs. 4 and 5 merely by the mechanical pressure of the large endosperm. In other words, the sheath of monocotyledons is probably a fusion of two or more cotyledons; the probability amounting almost to a certainty when we remember that the very same condition here described in a monocotyledon has been discovered in the dicotyledonous embryo of *Microcycas*, a complete fusion of the

two cotyledons. Looking at fig. 1 of pl. V in the *Microcycas* paper (14), and comparing it with my fig. 13, one would be puzzled to say which is the dicotyledon and which the monocotyledon. The same difficulty would arise by comparing my fig. 10 with fig. 13 of pl. VI of the *Microcycas* paper. Sister HELEN ANGELA was so impressed with the complete fusion of the two cotyledons that she called the fused structure a sheath.

Furthermore, a consideration of the vascular connections, the four root poles with their extensions finding full outlet in the sheath, shows that this sheath represents the whole cotyledonary apparatus, which, historically, finds its expression in many cotyledons in *Pinus*, in two in the normal cycads and dicotyledonous angiosperms, and in the sheath of monocotyledons.

This condition seems to me almost the last proof necessary to demonstrate the origin of monocotyledons from dicotyledons.

Summary

1. The embryo sac of *Cyrtanthus* seems to follow the regular *Lilium* type. The endosperm is very extensive.

2. Stomata are more numerous on the inner than on the outer surface of the carpel.

3. There are three separate bundles at the midrib of each carpel and two at the fusion of the carpels. This arrangement is related to the various parts of the flower.

4. The youngest observed stages of the embryo have the stem tip enveloped by a sheath with four lobes at its top.

5. In an older embryo the sheath is differentiated into a longer and a shorter side, the appearance and vascular anatomy of which give the distinct impression of two cotyledons.

6. Any pressure or fusion is referred to the extraordinary amount of endosperm.

7. The investigation is considered a last proof of the theory of monocotyledony from dicotyledony.

Coulter and Dr. W. J. G. Land for kind assistance during the early part of the investigation, and to Sister Helen Angela under whose direction it was completed.

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EXPLANATION OF PLATE XXIV

The drawings were made with the aid of an Abbé camera lucida, the magnification used being 120 diameters. In every case, *a* indicates the tip of the aborted or short side of the sheath, *c* the longer side, and *s* the space within the sheath.

Fig. 1.—Exterior view of a young embryo before the differentiation of the two portions of the sheath.

FIG. 2.—Longitudinal section through the center of the embryo shown in fig. 1.

FIG. 3.—Cross-section of a young sheath above the region of the growing point of the stem.

FIG. 4.—Exterior view of an older embryo, showing differentiation of both sides of the sheath.

FIG. 5.—Longitudinal section (partly reconstructed and diagrammatic), showing the first leaf, the growing point, and the behavior of the vascular bundles.

FIG. 6.—Cross-section through the root cylinder of the older embryo.

FIG. 7.—Cross-section of the cotyledonary node, showing the independent origin of the four bundles.

FIG. 8.—Cross-section just above the cotyledonary plate; the four bundles have assumed the vertical position.

FIG. 9.—Cross-section above that represented in fig. 8, showing the stem cylinder.

FIG. 10.—Section above the preceding, showing the first leaf and the growing point.

FIG. 11.—Cross-section above the tip of the second leaf.

FIG. 12.—Cross-section just above that shown in fig. 11; it shows the tip of the first leaf.

FIG. 13.—Cross-section above the tip of the first leaf; shows the space or slit between the two sides of the sheath.

FIG. 14.—A section showing the fusion of the four bundles to make two; it was made immediately above that shown in fig. 13.

FIG. 15.—A section near the tip of the aborted side of the sheath, giving the appearance of two cotyledons lying side by side.

FIG. 16.—A cross-section in the upper part of the sheath.